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Prey Capture in *Lyonsiella formosa* (Bivalvia: Anomalodesmata: Verticordiacea)[1]

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ABSTRACT: A specimen of the bathyal verticordiid *Lyonsiella formosa* has been obtained from Hawaii at 460 m depth. Assignment of this specimen to *L. formosa* suggests that this species has a much wider range than hitherto believed.

Dissection and subsequent histological examination of the specimen suggests a mechanism of prey capture completely different from that previously described for this species and resembling that attributed to *Poromya granulata*. Sensory papillae on the siphonal tentacles probably detect the prey. Prey capture is by eversion of an enormous hoodlike cowl of the inhalant siphon. Inversion brings the prey into the mantle cavity. Further distension of the siphon within the mantle cavity is believed to push the prey into the buccal apparatus comprising medially fused labial palps. The unfused tips of the palps or the foot may assist in this.

A model of the hydraulic changes that may occur in *Lyonsiella formosa* to effect prey capture is described. The similar modes of feeding exhibited by *L. formosa* (Verticordiidae) and *Poromya granulata* (Poromyidae) suggest a close affinity.

ON THE DEEP OCEAN FLOOR two bivalve taxa have adopted a predatory mode of life. Possibly all species of the Propeamussiidae are carnivores (Knudsen 1970, 1979), though the mechanism of prey capture is unknown. Conversely, the Parilimyidae, Verticordiidae, Poromyidae, and Cuspidariidae of the ancient and peculiar subclass Anomalodesmata have well-known predatory habits. Each species has particular morphological adaptations to its predatory life style, but the single most important feature of them all is the active muscular pumping of fluids in and out of the mantle cavity, to facilitate prey capture, instead of the ciliary movement of fine suspended material. The prey is digested by proteolytic enzymes (Reid 1977) within a highly modified gut (Purchon 1956). Yonge (1928) investigated *Poromya* and *Cuspidaria* but Reid and Reid (1974) were the first to demonstrate the mechanism of prey capture in *Cuspidaria*. This was subsequently confirmed by Allen and Morgan (1981) who also investigated poromyids but could not elaborate on the mechanism of prey capture. Feeding in *Poromya* was explained by Morton (1981*a*) who showed that the inhalant siphon comprised a huge raptorial cowl beneath which prey were trapped before being withdrawn into the mantle cavity. Morton (1981*b*) also explained prey capture in *Parilimya*, the raptorial inhalant siphon this time being withdrawn by elongate siphonal (taenioid) retractor muscles. Allen and Turner (1974) investigated the Verticordiidae in great detail but did not come to any firm conclusions with regard to how prey is captured, stating that (p. 513) "the tentacles in *L. abyssicola* and probably in all other species, extend across the surface layer of the abyssal sediment in life and passively wait for organisms to brush against them and adhere to them"; and later (also p. 513) "the tentacles with adhering food contract and move inwards into the inhalant aperture where they are wiped clean by the constriction of the inhalant aperture and valve—when the latter is present." This view was later reiterated by Allen (1983).

Allen and Turner (1974) describe a variety of siphonal types for the verticordiids they investigated, suggesting a greater diversity of feeding strategies than sticky tentacles. Ac-

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cordingly, *Lyonsiella formosa* is here investigated in greater detail, special attention being paid to the possible mechanism of prey capture.

TAXONOMY

Lyonsiella formosa (Jeffreys, 1881) has been further described by Allen and Turner (1974) who also illustrated the structure of the body as well as the shell. The species has only been recorded from the Atlantic (i.e., the Canaries, Azores, Bay of Biscay, and Gulf of Mexico) at depths ranging between 366 and 3783 m (Allen and Turner 1974, Knudsen 1979). I have also examined the type specimen (AMNH Reg. no. 61238).

Lyonsiella elegans (Thiele and Jaeckel, 1931) has only been recorded from the type locality, Station 242 (404 m) of the *Valdivia* Expedition (1898–1899) (6° 34.8′ S, 39° 35.5′ E) at Dar es Salaam. I have not seen the type specimen of this species, there being an excellent illustration of it (Thiele and Jaeckel 1931).

Thiele and Jaeckel acknowledge that *Lyonsiella elegans* resembles the Atlantic *L. formosa*, and Allen and Turner (1974) have shown that the shells of different-sized specimens of the latter species vary considerably in overall form and in details of the sculpture. The specimen here under consideration was obtained from a depth of 460 m off Hawaii and bears a very strong resemblance to *L. elegans*. Bearing in mind the great variability in shell form of *L. formosa*, however, and assuming that *L. elegans* is possibly equally variable, it seems very probable that *L. elegans* is but a junior synonym of *L. formosa*. As will be seen later, the specimen is morphologically indistinguishable from *L. formosa*. It accordingly seems likely that *L. formosa* is not restricted to the Atlantic, but is a widely distributed bathyal species.

MATERIALS AND METHODS

The specimen of *Lyonsiella formosa* here investigated was obtained during a short research visit to Hawaii in December 1981 with a box dredge operating at a depth of 460 m and with a sea temperature of 9° C. No observations on the living animal were possible, as it was dead by the time the dredge reached the surface. It was preserved in 5 percent neutral formalin. Following dissection, the specimen was transversely sectioned at 6 μm and alternate sections stained in either Ehrlichs' haematoxylin and eosin or Masson's trichrome. The broken shell has been deposited in the collections of the Bernice P. Bishop Museum (Reg. no. 207491).

FUNCTIONAL MORPHOLOGY

The Shell

The shell (Figure 1A) is exceedingly fragile, equivalve, and markedly inequilateral. The anterior face is rounded and somewhat reduced relative to the posterior which is inflated. The posterior margin is ventrally angular and has a corrugated outline. Whereas the anterior face is smooth, the posterior is radially ridged and concentrically ringed. From each umbone arises a single rib that extends to the ventral margin just posterior to the mid line. Seven or eight further rays extend to the posterior and posterodorsal margin of the shell.

At the junction of each ray with a concentric ring a sharp spine is produced, though in this specimen most have been broken off. Spines in different positions adorn the shells of *Lyonsiella formosa* illustrated by Allen and Turner (1974), but a series of spines on the dorsal part of the shell appear more resistant and characterize all individuals, including the type of *L. elegans* (Thiele and Jaeckel, 1931). The shell between the posterior rays and the single more median rib is concave. Allen and Turner (1974) illustrate exceedingly fine rays on the anterior face, these are barely discernible in this specimen. The surface of the shell is finely grained. From the dorsal aspect (Figure 1B) the great expansion of the posterior region of the shell is more clearly seen. This results from, as will be seen later, the location of the prey-capturing organs posteriorly. The shell is widely emarginate posteriorly and less

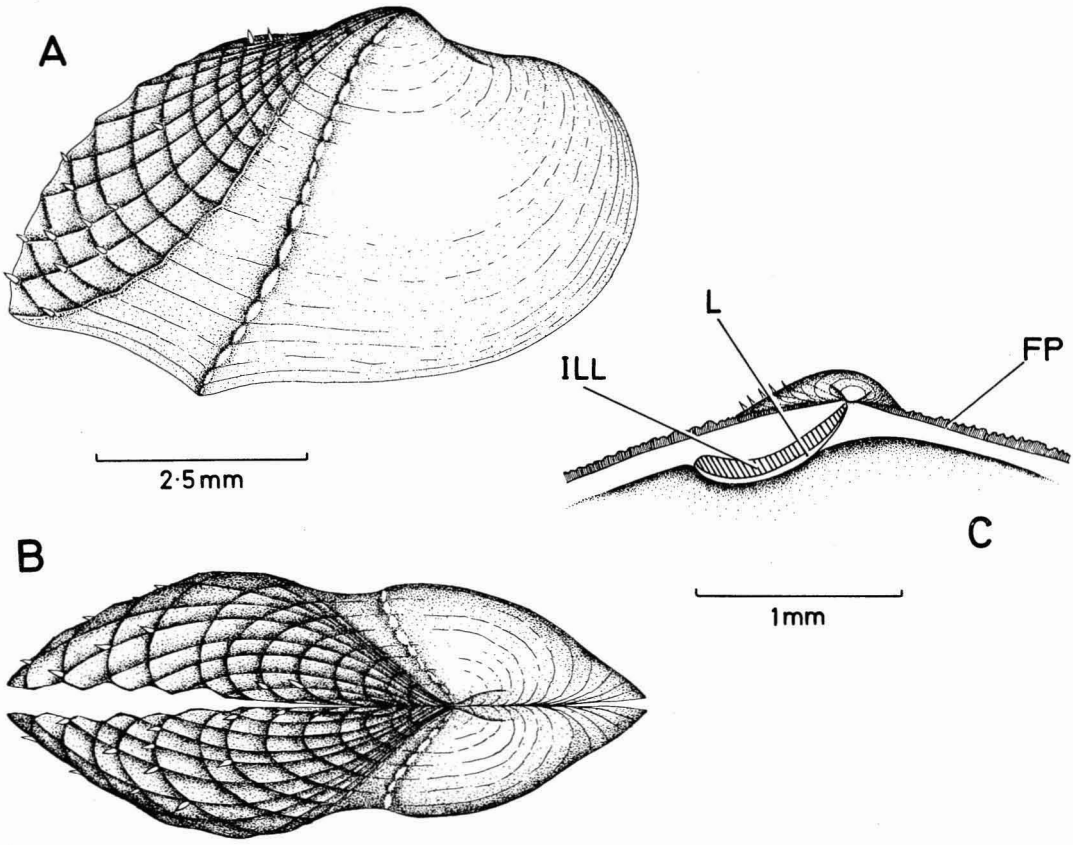

FIGURE 1. *Lyonsiella formosa*. The shell as seen from A, the right side, and B, the dorsal aspect; C, an enlarged view of the hinge plate of the left valve. *FP*, fused periostracum; *ILL*, inner ligament layer; *L*, lithodesma.

so anteriorly. The umbones point slightly forward.

Hinge structure has similarly been described by Allen and Turner (1974) (Figure 1C). There are no hinge teeth. The primary ligament is small and internal, comprising inner ligament layer (*ILL*) only, this being calcified mid-ventrally into an inconspicuous lithodesma (*L*). The dorsal borders of the shell are united by a thin layer of fused periostracum (*FP*) forming a "secondary" ligament whose main function is to assist in the alignment of the valves.

The Musculature

The two adductor muscles (Figure 2, *AA*; *PA*) are of approximately equal size (isomyarian) and are bordered internally by very tiny pedal retractor muscles—anterior (*APR*) and posterior (*PPR*). Other muscles are concerned with pallial retraction (Figure 7A, *PRM*). From the exhalant siphon extends a thin array of muscles (Figure 2, *ESR*) which posteriorly attach to the shell approximately where the dorsal margin of the ascending lamella of the outer demibranch unites with the mantle.

The inhalant siphon is retracted by a pair of muscles within the fused ventral mantle margin and which have their origins posterior to the pedal gape. The muscles are attached at the single near-median rib on each valve and extend posteriorly into the inhalant siphon, radiating as they do.

Since the muscles are probably derived from the more typical bivalve siphonal retractor system, these are called taenioid muscles

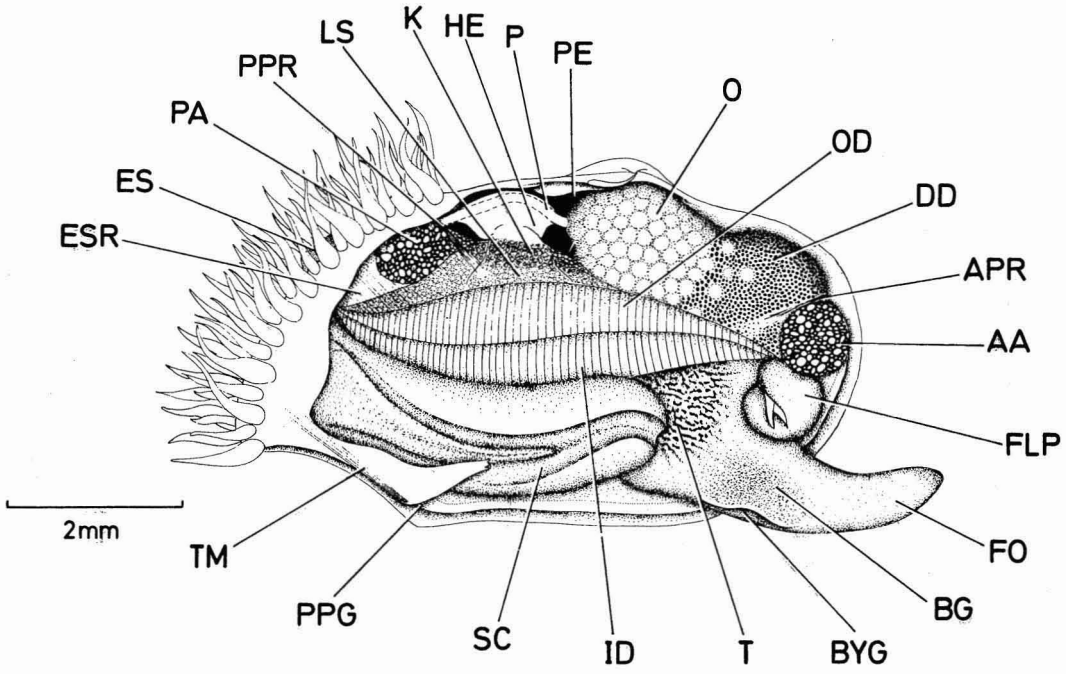

FIGURE 2. *Lyonsiella formosa.* The organs of the mantle cavity after removal of the right shell valve and mantle lobe. *AA*, anterior adductor muscle; *APR*, anterior pedal retractor muscle; *BG*, byssal gland; *BYG*, byssal groove; *DD*, digestive diverticula; *ES*, exhalant siphon; *ESR*, exhalant siphonal retractor muscle; *FLP*, fused labial palps; *FO*, foot; *HE*, heart; *ID*, inner demibranch; *K*, kidney; *LS*, lacunal system; *O*, ovary; *OD*, outer demibranch; *P*, periostracum; *PA*, posterior adductor muscle; *PE*, pericardium; *PPG*, posterior limit of pedal gape; *PPR*, posterior pedal retractor muscle; *SC*, siphonal cowl; *T*, testis; *TM*, taenioid muscle.

(Figure 2, *TM*), and can be compared with those of *Lyonsiella fragilis* (Allen and Turner 1974) and *Parilimya fragilis* (Morton 1981*b*).

The Siphons

The siphons of *Lyonsiella formosa* are pale cream and surrounded by a ring of approximately 48 tentacles arranged in two cycles; those of the outer cycle are larger and longer than those of the inner. The appearance of the siphonal apparatus as seen from the posterior aspect is shown in Figure 3. Allen and Turner (1974) record a maximum number of 45 tentacles. Each tentacle is profusely papillate. Allen and Turner have described the structure of a tentacle as comprising a central core of tissue containing a subdivided hemocoel and surrounded but separate from the outer epithelium by yet a further hemocoel. I believe this to be an artifact and that in life there is no outer hemocoel separating epithelium from the central tissues, and I believe the structure to be basically the same as that described for *Poromya* by Morton (1981*a*). Thus, the enclosing epithelium is formed into numerous small projections or papillae that are sensory (Figure 4A, *SP*). Internally there is a large nerve (*N*) surrounded proximally by but a few longitudinal muscle fibers, and from between it and a large hemocoelic space (*H*) arise an array of radial muscle fibers (*RM*) that extend to the outer epithelium and are separated from each other by numerous smaller hemocoelomic spaces. At higher resolution (Figure 4B), each papilla comprises conical cells surrounding a flask-shaped chamber (*CH*). Arising from the base of this chamber is a single, long (8 μm) flagellum (*F*). It may be that there is more than one flagellum, but if so I cannot differentiate them, as has been possible by electron microscopy for *Laternula*

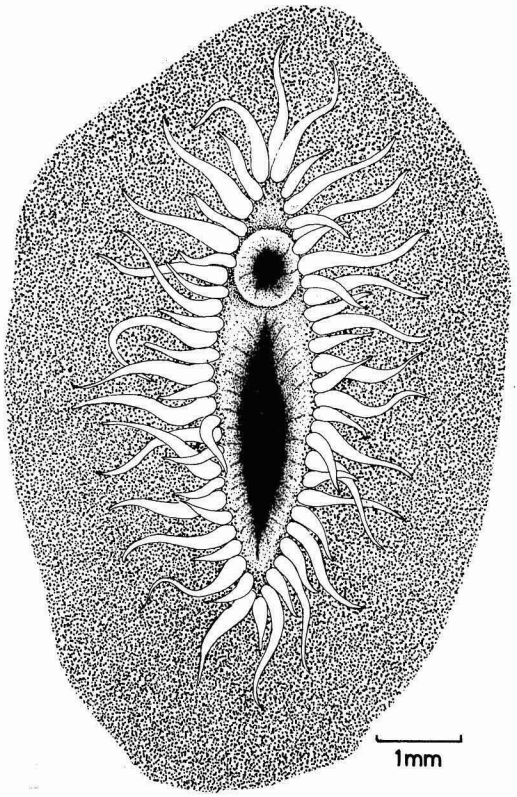

FIGURE 3. *Lyonsiella formosa.* The siphons and siphonal tentacles as seen posteriorly with the shell buried in sand. The exhalant siphon is dorsal.

and *Cardiomya* (Adal and Morton 1973, Reid and Crosby 1980) in which somewhat similar but much larger sense organs occur at the apex of each tentacle. The tentacles of *Lyonsiella* have a structure almost identical to those of *Poromya* (Morton 1981*a*), including most importantly the ciliated sense organs on the papillae.

Allen and Turner (1974) describe *Lyonsiella formosa*, and other verticordiids, as possessing a large valve to the inhalant siphon. Yonge (1928) and Bernard (1974) also thought *Poromya granulata* and *P. tenuiconcha* possessed a similar structure. Morton (1981*a*), however, showed for *P. granulata* that the "valve" was in fact the inverted inhalant siphon, with the tentacles surrounding the base of this structure. This is also true of *L. formosa.* The "valve" comprises a deeply folded siphonal cowl (Figure 2, *SC*), or hood, that is open ventrally, not dorsally as suggested for this species by Allen and Turner (1974). At the tip and in transverse section (Figure 5A), the hood comprises an inner (*IE*) and outer (*OE*), much folded, squamous epithelium, cross-connected by fine transverse muscle fibers (*TF*). Internally, there is an enormous hemocoel (*H*). Further toward the posterior base of the siphon (Figure 5B), the hood becomes penetrated by the radiating longitudinal fibers of the taenioid muscles (*LM*). There is still an extensive hemocoel (*H*) and the enclosing, much less folded epithelia are cross-connected by thicker transverse muscle fibers (*TF*). It is suggested that the hood of the inhalant siphon can be everted in much the same way as that of *Poromya* to ensnare the prey beneath it. This is illustrated in Figure 6, and the mechanism of prey capture will be discussed later.

The Mantle

The inner and outer pallial epithelia are widely separate as in *Cuspidaria* except that in the latter, wide separation only occurs dorsal to the point of union of the septum with the mantle (Reid and Reid 1974). In *Lyonsiella* the mantle epithelia are everywhere, except laterally, widely separate (Figure 7A) and cross-united by strands of muscle fibers (*TF*). Underlying the inner epithelium is an extensive eosinophilic unicellular gland that also stains dark green in Masson's trichrome (Figure 7A, *MG*; Figure 7B). Anteriorly the gland is sparse, but increases in size posteriorly so that it virtually completely lines both supra- and infrabranchial chambers (Figures 9 and 10, *MG*). A similar gland is seen in *Poromya* but there it only lines the supraseptal chamber (Morton 1981*a*). The epithelium of the general mantle surface is unciliated.

The pedal gape is long, extending from beneath the anterior adductor muscle to a point on the shell margin where the single near-median rib demarcates a change in shell form (Figure 2, *PPG*). The mantle margin of the pedal gape (Figure 7) is exceedingly simple, comprising unspecialized inner (*IMF*), middle (*MMF*), and outer (*OMF*)

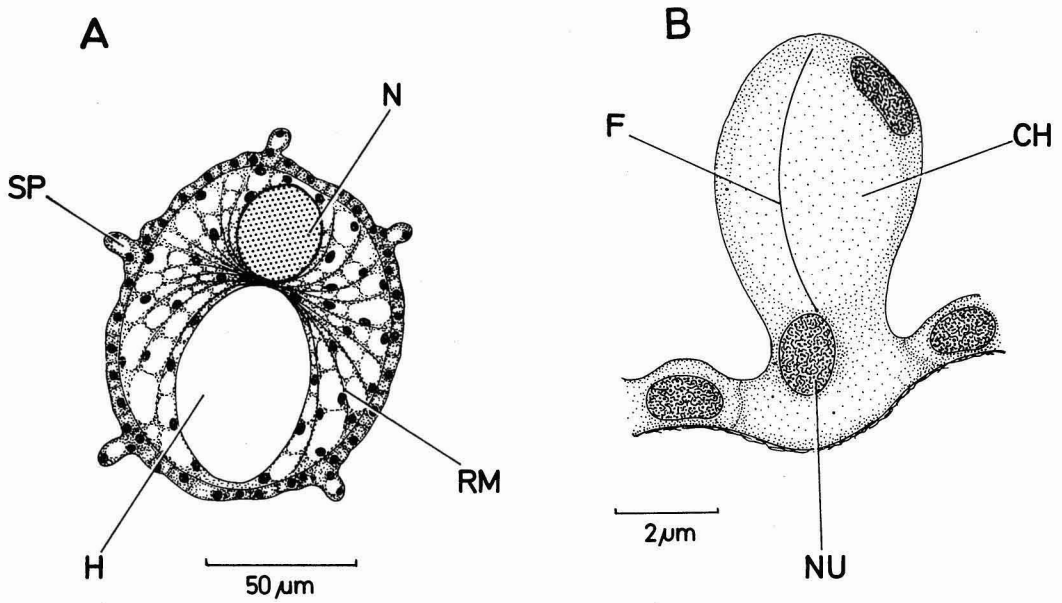

FIGURE 4. *Lyonsiella formosa.* A, a transverse section through a single siphonal tentacle; B, detail of a single sensory papilla of a siphonal tentacle. *CH*, chamber; *F*, flagellum; *H*, hemocoel; *N*, nerve; *NU*, nucleus; *RM*, radial muscle fibers; *SP*, sensory papilla.

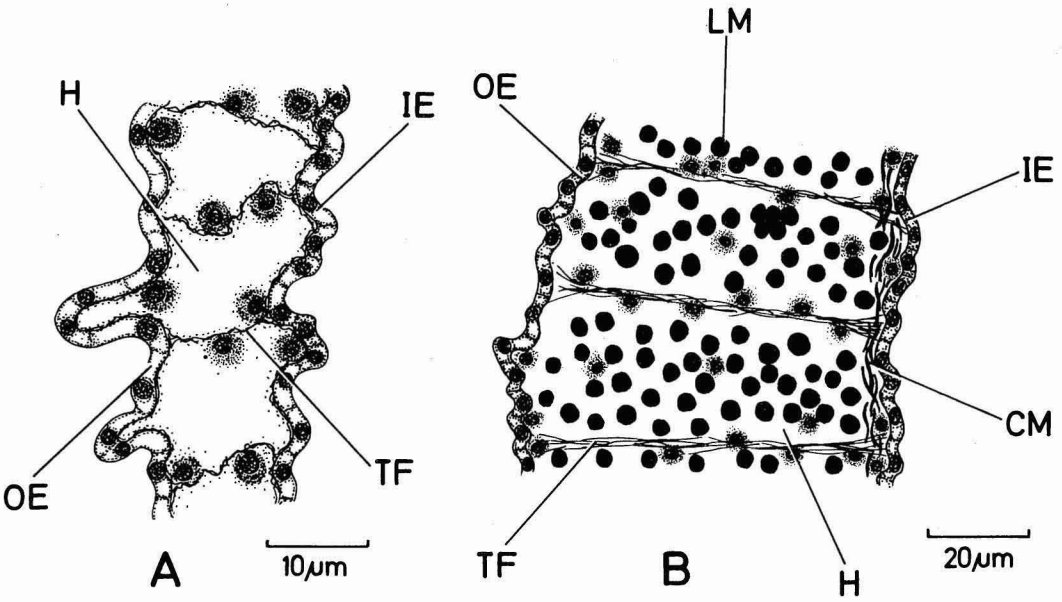

FIGURE 5. *Lyonsiella formosa.* Transverse sections through the wall of the siphonal cowl; A, at its tip (note the absence of longitudinal muscles); and B, at its base. *CM*, circular muscle fibers; *H*, hemocoel; *IE*, inner epithelium; *LM*, longitudinal muscles; *OE*, outer epithelium; *TF*, transverse muscle fibers.

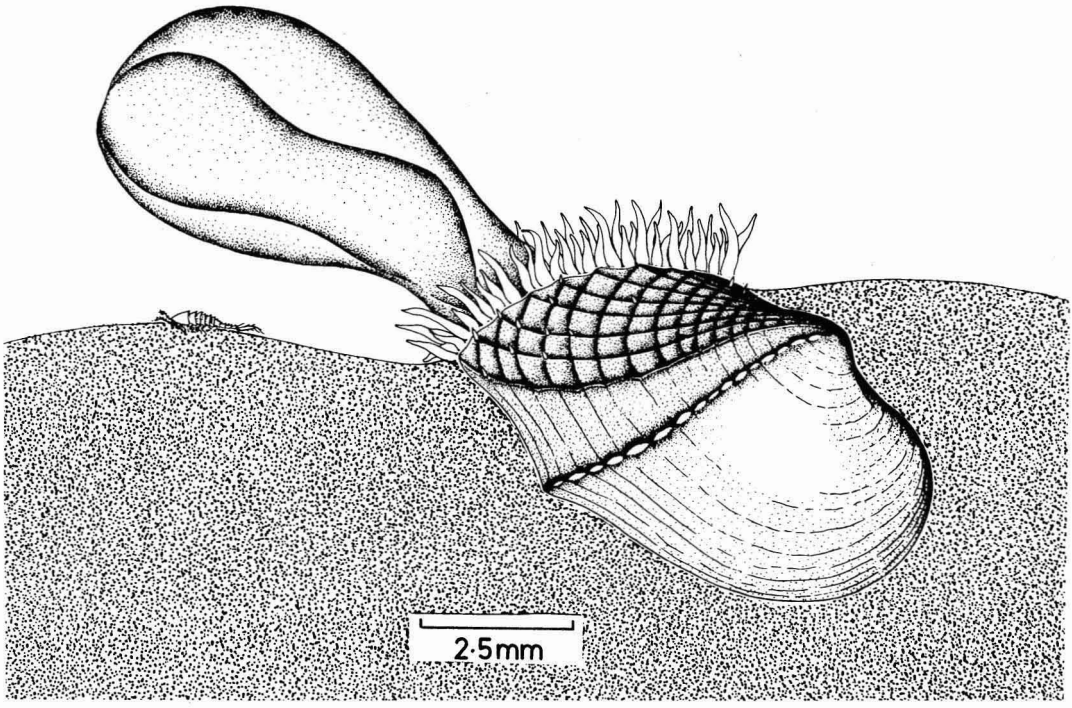

FIGURE 6. *Lyonsiella formosa.* The animal in a natural position in the sediment and with the inhalant cowl of the siphon fully extended. The animal is here illustrated capturing a bottom-dwelling copepod. This has not been observed, but is the interpreted feeding mechanism.

folds. A pallial retractor muscle (*PRM*) extends into the margin. There are no glands and there is an extensive hemocoel (*H*). Posteroventrally (Figure 8) left and right union of the mantle lobe margins is by fusion of the inner and middle folds (Type *B*) (Yonge 1982), these forming a small ridge (*FMMF*) extending between greatly enlarged outer folds (*OMF*). A thin periostracum (*P*) arises from the periostracal groove (*PG*). The mantle margins also have an enormous hemocoel, the two epithelia being joined laterally and centrally by transverse muscle fibers (*TF*). The central zone of fusion is characterized by the pair of large siphonal retractor muscles (taenioid muscles) (*TM*) earlier described. The inner surface ventrolaterally comprises two rows of ciliated columnar cells. These longitudinal tracts (*RT*) presumably collect fine material that might inadvertently enter the mantle cavity during feeding, and transport it either to the inhalant siphon (as in conventional bivalves) for disposal, or possibly, in this raptorial species, in an anterior direction to the pedal gape. In *Cuspidaria*, however, pseudofeces are still ejected from the inhalant siphon (Reid and Reid 1974).

The Ctenidia and Labial Palps

The ctenidia (Figure 2) are of the typical anomalodesmatan plan comprising an entire inner demibranch (*ID*) and the ascending lamella only of the outer demibranch (*OD*). An important difference is that whereas in the typical anomalodesmatan, the ctenidia are vertically aligned, in *Lyonsiella* they are horizontal (Figures 9 and 10). The ctenidia are reduced and the horizontal orientation largely concerns itself with the posterior regions of the body where the shell is inflated (Figure 9, *CF*). Horizontal positioning is also permitted by the fact that, as in all anomalodesmatans hitherto studied (Morton 1981*c*), the ctenidial axis (*CA*) separates from the visceral mass posteriorly, coincidentally forming a capaci-

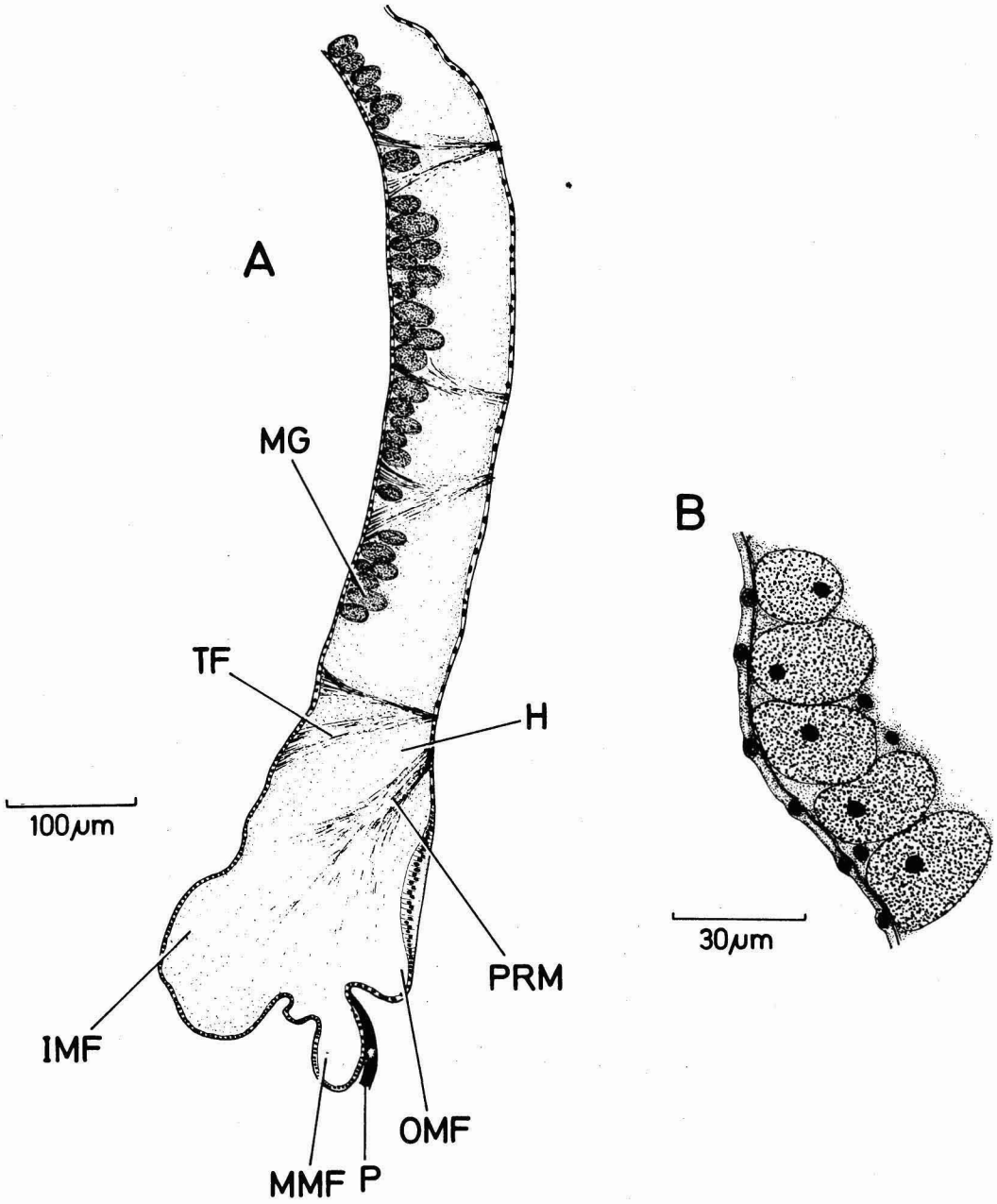

FIGURE 7. *Lyonsiella formosa*. A, a transverse section through the right mantle lobe margin; B, detail of the mucous glands in the mantle. *H*, hemocoel; *IMF*, inner mantle fold; *MG*, mucous gland; *MMF*, middle mantle fold; *OMF*, outer mantle fold; *P*, periostracum; *PRM*, pallial retractor muscle; *TF*, transverse muscle fibers.

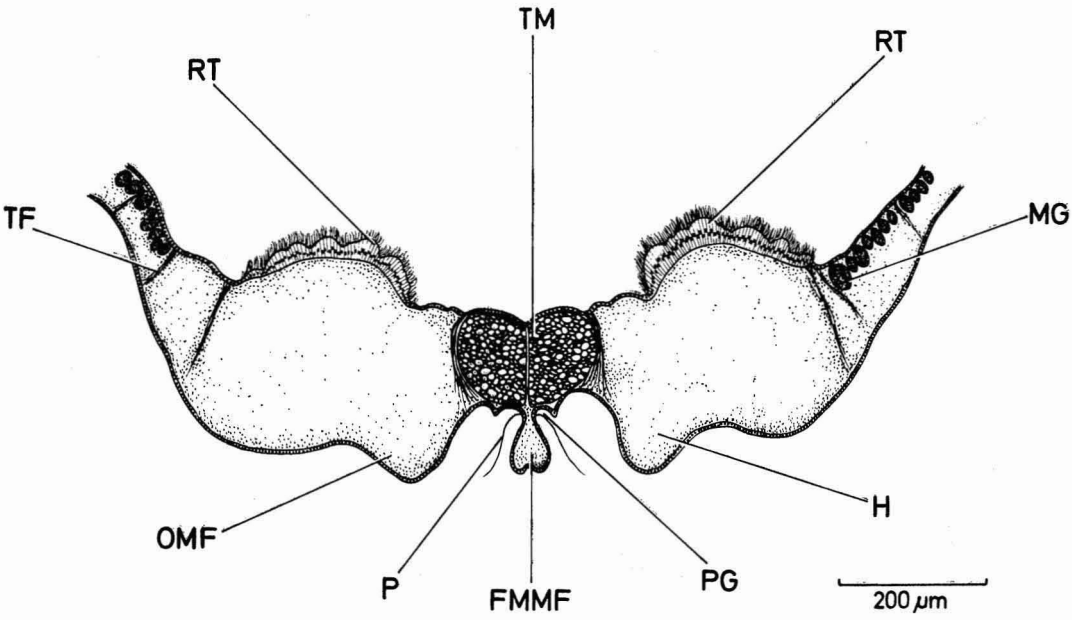

FIGURE 8. *Lyonsiella formosa.* A transverse section through the fused mantle margins posterior to the pedal gape. *FMMF*, fused middle mantle folds; *H*, hemocoel; *MG*, mucous gland; *OMF*, outer mantle fold; *P*, periostracum; *PG*, periostracal groove; *RT*, rejectory tract; *TF*, transverse muscle fibers; *TM*, taenioid muscle.

ous suprabranchial chamber and with important implications for the evolution of the poromyid and cuspidariid septum. As in other anomalodesmatans the ascending lamella of the inner demibranch is but weakly attached to the visceral mass.

The labial palps of *Lyonsiella formosa* (Figure 2, *FLP*) are complex and have been described by Allen and Turner (1974). Essentially, inner and outer palps are fused into a pouch that opens laterally in a pair (left and right) of fluted funnel-shaped tubes which correspond to the separated palp tips. The ctenidia terminate in these orifices. The complex structure of the palps means that they cannot be dramatically extended as in *Poromya* to seize prey in the mantle cavity (Morton 1981*a*). Rather, prey must be taken to them, as will be discussed.

The Foot, Visceral Mass, and Pericardium

The foot (Figure 2, *FO*) is long and clearly functions as a digging tool. There is a distinct byssal groove (*BYG*) mid-ventrally and a functional byssal gland (*BG*) but no byssal threads. Within the visceral mass there is an ovary (*O*) and a testis (*T*) (i.e., *Lyonsiella formosa* is a simultaneous hermaphrodite as in most anomalodesmatans; Morton 1981*c*). The heart (*HE*) lies posterior to the umbones and comprises a central ventricle, penetrated by the rectum (*R*), and lateral auricles. Beneath it lies the paired kidney (*K*), the distal limbs being enormous and the cells occupied by spherical excretory granules. Surrounding each kidney, however, is a large, complex, system of lacunae (*LS*), that in life are white and could superficially be mistaken for the kidney, which they obscure. Much of the posterior inflation of the shell accommodates this system. Allen and Turner (1974) described this lacunal system for *L. abyssicola* and showed that the situation in *L. formosa* is essentially the same. The lacunal system in fact occupies the mantle (Figures 9 and 10), proliferating around the kidney and extending down into the mantle enclosing the suprabranchial chamber. The lacunal system, on first inspection, appears to be a gland (Figure 10B), but close inspection reveals the absence of any secretory surfaces and the thin-walled lacunae (*LW*) contain

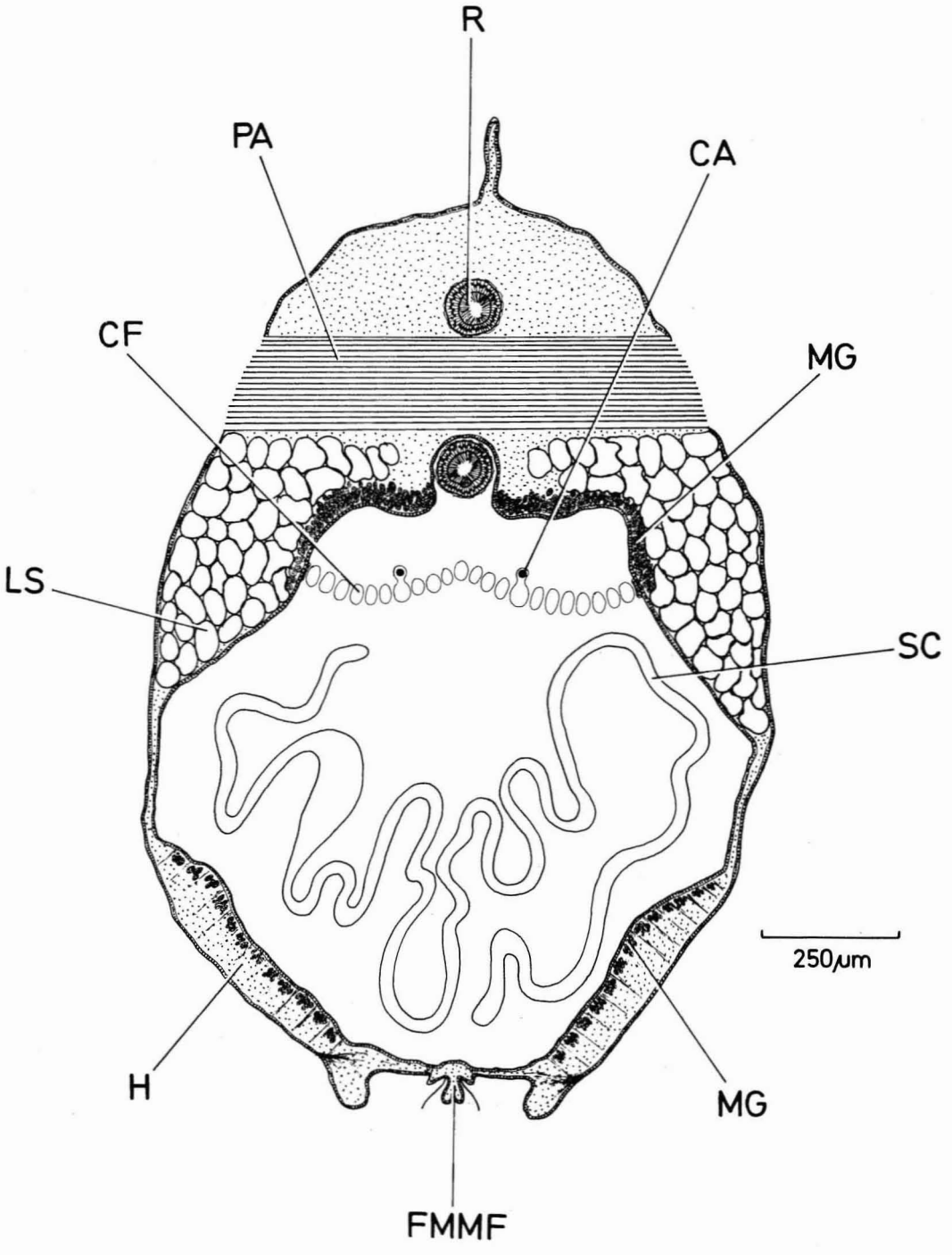

FIGURE 9. *Lyonsiella formosa*. A transverse section through the whole body at the posterior adductor muscle and point of ventral mantle fusion posterior to the pedal gape. *CA*, ctenidial axis; *CF*, ctenidial filament; *FMMF*, fused middle mantle folds; *H*, hemocoel; *LS*, lacunal system; *MG*, mucous gland; *PA*, posterior adductor muscle; *R*, rectum; *SC*, siphonal cowl.

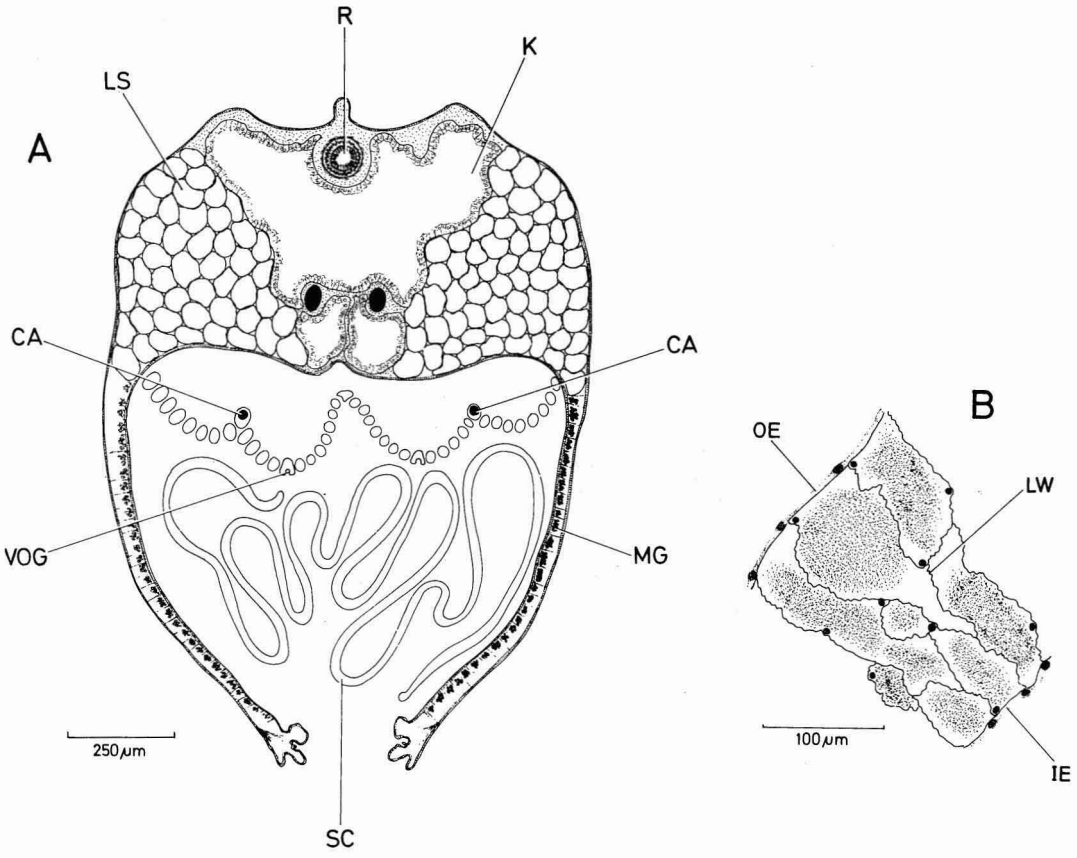

FIGURE 10. *Lyonsiella formosa.* A, a transverse section through the whole body in the region of the kidney and lacunal system; B, a detail of the lacunal system. *CA*, ctenidial axis; *IE*, inner epithelium; *K*, kidney; *LS*, lacunal system; *LW*, lacunal wall; *MG*, mucous gland; *OE*, outer epithelium; *R*, rectum; *SC*, siphonal cowl; *VOG*, ventral oral groove.

blood cells. The significance of this lacunal system will be discussed.

DISCUSSION

As currently recognized, there are four families of anomalodesmatan predators—the Parilimyidae, Verticordiidae, Poromyidae, and Cuspidariidae—each, save the former, presently located in its own superfamily (Morton 1981*c*). The Parilimyidae for a number of reasons are regarded as belonging to the ancient Pholadomyacea, and Morton (1981*b*) has suggested that these bivalves are primitive, with representatives later giving rise to the more advanced families of predatory anomalodesmatans.

The method of prey capture in *Lyonsiella formosa* has not been described, but based on this study it seems clear the notion that tentacles around the siphonal orifices are "sticky" to entrap prey (Allen and Turner 1974) is not true. The tentacles possess no glands. Nor, importantly, do the tentacles surround the apex of the siphons as suggested by Allen and Turner (1974) for this species and by Yonge (1928) for *Poromya.* Rather, as in *Poromya* (Morton 1981*a*), the tentacles surround their bases.

Moreover, the tentacles of both *Poromya* and *Lyonsiella* possess flagellate sense cells that presumably detect the presence of prey as postulated for *Cuspidaria* and *Cardiomya* by Reid and Crosby (1980). Also, like *Poromya*,

the inhalant siphon is deeply inverted into the infrabranchial chamber. Both Yonge (1928) for *Poromya* and Allen and Turner (1974) for the Verticordiidae thought it formed an internal "valve" but, in fact, as in *Poromya* (Morton 1981*a*), the "valve" can be everted far beyond the ring of basal tentacles and formed into a hood, beneath which, it is postulated, the prey is trapped. Retraction of the siphon will bring the prey into the infrabranchial chamber, as in *Poromya*. A major difference between *L. formosa* and *P. granulata*, however, lies in the fact that the labial palps of the former are formed into a fused, medial sac, only the tips forming narrow fluted funnels laterally. In the latter, the anterior palps are capable of great extension and, reaching back into the mantle cavity, can grasp the prey and stuff it into the mouth. This cannot be so in *L. formosa* and it is suggested that in this animal, the inhalant siphon may extend forward and push food into either one of the lateral funnels leading to the mouth. Possibly the palp tips are capable of some distension to assist in this or, as suggested by Bernard (1974) for *Poromya tenuiconcha*, the highly active foot has some role in this process.

Figure 11 attempts to interpret the mechanism of prey capture in *Lyonsiella formosa*. Three hemocolic spaces are important: (1) the lacunal system, (2) the pallial hemocoel, and (3) the hemocoel of the inhalant siphon. In the resting condition, the bivalve presumably functions like any other, valve movements and the eulaterofrontal cilia of the ctenidial filaments creating a respiratory flow (Figure 11A). The locomotory movements of the prey are presumably detected by the sense organs on the tentacle papillae, as in *Cuspidaria*, *Cardiomya*, and *Poromya* (Reid and Reid 1974, Reid and Crosby 1980, Morton 1981*a*) (Figure 11B).

Once the prey is detected, the prey-capturing process is initiated (Figure 11C). Since this involves eversion of the inhalant siphonal hood by hydraulic pressure changes in the body, the following process, based upon the structure of the various hemocoelic spaces, is postulated.

Adduction compresses mantle fluids and the blood within the lacunal system. Blood is therefore forced into the pallial hemocoels, filling them. Overfilling is prevented by the transverse muscle fibers cross-connecting the two epithelia. From here blood is then forced into the siphonal hood causing it to evert and to entrap the prey (Figure 11C). The siphon can be everted from between the shell valves even though they are closed, because of their wide emargination posteriorly. The siphon, with prey, is returned to the mantle cavity by relaxation of the adductor muscles so that the valves part and internal pressures are neutralized. This causes blood to flow back from the siphon into the lacunal system so that the siphons can now be retracted by contraction of the taenioid muscles in the ventral mantle margin (Figure 11D). The prey has now to be transferred to the mouth, and as noted earlier this cannot be, as in *Poromya*, by great backward distension of the anterior palps to grasp the prey from the siphon, because in *Lyonsiella formosa*, the palps are medially fused into a buccal sac. It seems more likely that the siphon itself is extended anteriorly and passes the prey to the free tips of the palps which may in turn assist in stuffing the food into the mouth. Anterior extension of the siphon must be essentially the same as for eversion. Thus, closure of the valves again forces blood from the lacunal system reservoir into the siphon which expands within the mantle cavity (eversion being prevented, possibly by the sustained contraction of the taenioid muscles) pushing the food toward the palps (Figure 11E). Following ingestion the animal returns, by opening the valves and equalizing pressures throughout the body, to a balanced state (Figure 11F).

The foregoing mechanism of prey capture fits interpreted structure. Certainly with no glands in the tentacles, prey capture is not by "sticky" tentacles as proposed by Allen and Turner (1974) and Allen (1983). Rather, as in all predatory, deep water, anomalodesmatans hitherto studied, a raptorial inhalant siphon is everted as a result of induced pressure changes translocating blood from a reservoir into the siphon and its subsequent return by muscular retraction.

It is important that attempts be made to investigate living members of these predatory

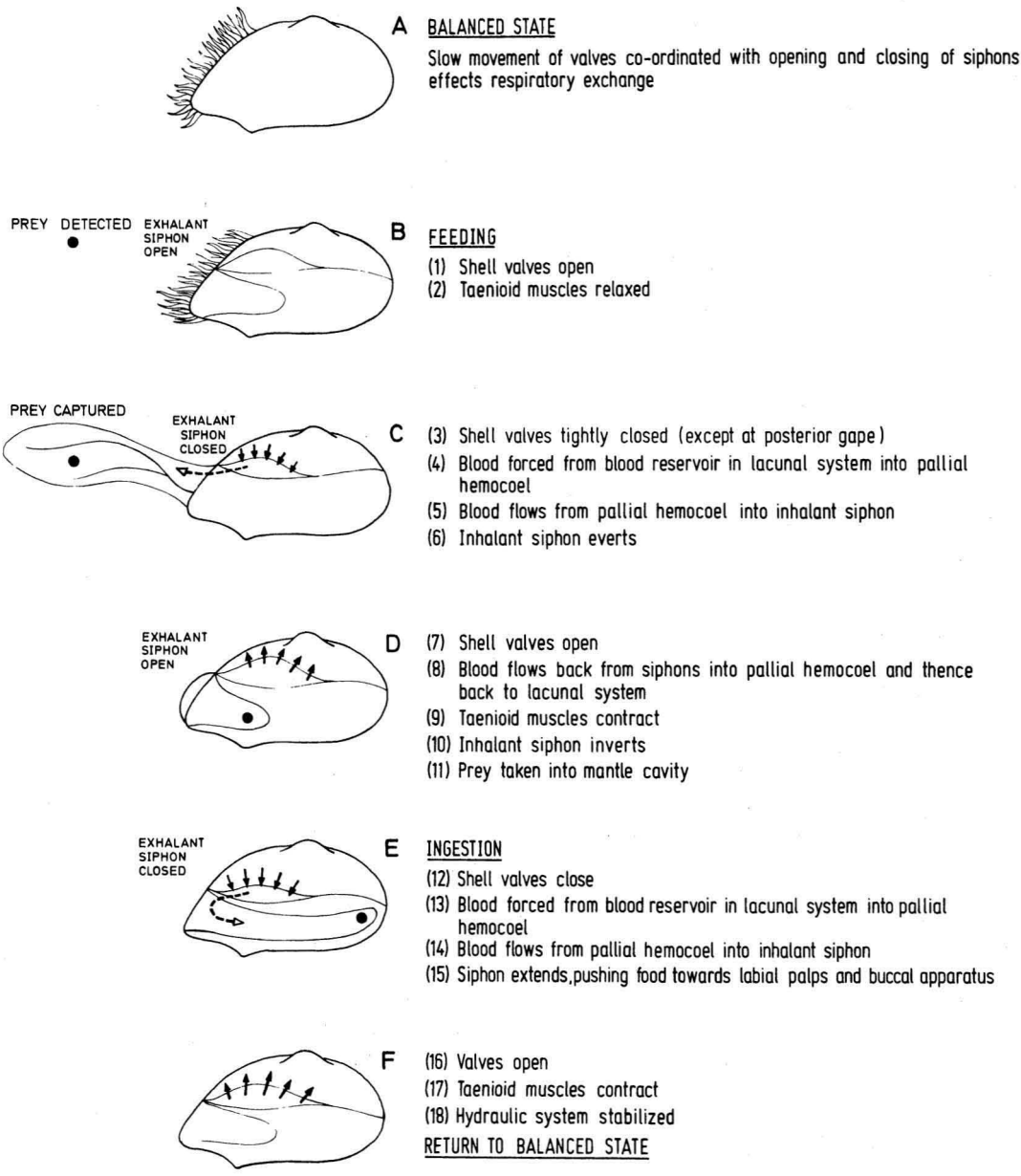

FIGURE 11. *Lyonsiella formosa.* The proposed mechanism of prey capture (for an explanation see text).

families to determine the precise mechanism of prey capture.

The relationships existing between the various families of predatory deep water bivalves is far from clear. Runnegar (1974) placed the Verticordiidae in the Pandoracea, believing them to have evolved from a lyonsiid-like ancestor. This view was also held by Allen and Turner (1974). Runnegar (1974) placed the Cuspidariidae in the Palaeotaxodonta—a now discredited notion (Yonge and Morton 1980) originally formulated by Purchon (1956)—leaving only the Poromyidae in the Poromyacea. Bernard (1974) believed the

group to comprise two superfamilies, the Verticordiacea (Verticordiidae) and the Poromyacea (Poromyidae and Cuspidariidae). Subsequently, however, Bernard (1979) has altered his views somewhat and now considers all three families to have superfamily status, the Verticordiacea (Verticordiidae and Lyonsiellidae) belonging to the order Pholadomyoida and the Poromyacea and Cuspidariacea belonging to the order Septibranchoida. Morton (1981*c*), reviewing such diverse opinions, preferred to maintain each family in its own superfamily but all within the single order Pholadomyoida. Allen and Morgan (1981) placed the Verticordiidae and Poromyidae in the Poromyacea and the Cuspidariidae in its own superfamily. Most recently Morton (1984) has reviewed statocyst structure in representatives of all, as currently recognized, anomalodesmatan familial lineages and has come to a similar conclusion. Thus, the statocysts of all species of *Cuspidaria* are different from those of representatives of the Verticordiidae and Poromyidae, arguing that the latter families are allied and distinct from the Cuspidariidae.

This study of prey capture in *Lyonsiella formosa* further substantiates this view. The feeding mechanisms of *Poromya* and *L. formosa* are almost exactly the same, and both are different from that described for *Cuspidaria* and *Cardiomya* (Reid and Reid 1974, Reid and Crosby 1980). Though Allen and Turner (1974) described the siphonal apparatus of many verticordiids, evaluations of how different species might feed are not given; all are presumed to have sticky tentacles. Morton (1981*b*) has pointed out the great similarity existing between the siphonal apparatus of *Lyonsiella fragilis* (Allen and Turner 1974, fig. 50) and that of *Parilimya fragilis* (Parilimyidae: Pholadomyacea) (Morton 1981*b*, figs. 8 and 9). Such a similarity argues for a close link between the Parilimyidae and the possibly least specialized Verticordiidae. It is clear that the Verticordiidae, as currently defined, possess a great variety of prey capture techniques. Each species will have to be examined in closer detail, and interpreted, in order to obtain a better understanding of the relationships existing not only between the various species but, also, of their origins and relationships with the other predatory anomalodesmatan bivalves.

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